

REVISION OF *LOBELIA* SECT. *PLAGIOBOTRYS* (CAMPANULACEAE: LOBELIOIDEAE)

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ABSTRACT

Lobelia sect. **Plagiobotrys** comprises large straggling or scrambling Malesian herbs and shrubs with elongate lateral racemes, bilabiate corolla, tufts of flattened trichomes at the apex of each anther, baccate fruit, and reticulate seeds. The type is *L. borneensis*, which is divided here into four allopatric subspecies: subsp. *borneensis* (Sarawak); subsp. **celebensis**, subsp. nov. (Sulawesi); subsp. **grandiflora**, comb. et stat. nov. (Sabah); and subsp. **insulae-florum**, subsp. nov. (Flores). Added to this is **L. origenes**, sp. nov., also from Sabah, but from higher elevations than *L. borneensis* subsp. *grandiflora*.

RESUMEN

Lobelia sect. **Plagiobotrys** comprende hierbas y arbustos grandes malesianos extendidas o reptantes con racimos laterales alargados, corola bilabiada, mechones de tricomas aplastados en el ápice las anteras, fruto baccáceo, y semillas reticuladas. El tipo es *L. borneensis*, que se divide aquí en cuatro subespecies alopátricas: subsp. *borneensis* (Sarawak); subsp. **celebensis**, subsp. nov. (Sulawesi); subsp. **grandiflora**, comb. et stat. nov. (Sabah); y subsp. **insulae-florum**, subsp. nov. (Flores). Se añade a esto **L. origenes**, sp. nov., también de Sabah, pero de mayores elevaciones que *L. borneensis* subsp. *grandiflora*.

INTRODUCTION

Lobelia L. is the largest of the 29 genera in the Lobelioideae (Campanulaceae) with over 400 species (Lammers 2007a, 2007b). Recently, I revised the infrageneric classification of the genus, recognizing 18 taxonomic sections (Lammers 2010a). Among those newly recognized was *L. sect. Plagiobotrys*, which contained but a single species, Malesian *L. borneensis*. However, in the course of examining representative material for that study, significant variation was noted among the exemplars of that species; this suggested that additional taxa referable to *L. sect. Plagiobotrys* might be lurking undetected and that further study was warranted. This research has been completed and its results presented here, as the fifth in a series of species-level accounts for the sections of *Lobelia*. Previous entries in the series covered *L. sect. Tupa* (G. Don) Benth. (Lammers 2000), *L. sect. Homochilus* A. DC. (Lammers 2004), *L. sect. Galeatella* E. Wimm. (Lammers 2007c), and *L. sect. Speirema* (Lammers 2010b).

TAXONOMIC HISTORY

The history of *Lobelia* sect. *Plagiobotrys* begins with the description of *Pratia borneensis* by William Botting Hemsley of the Royal Botanical Gardens, Kew. This name was based upon a specimen collected on Borneo in August 1884 by Singapore schoolmaster R. William Hullet, which was included among a group of 280 specimens sent to Kew a year later (van Steenis-Kruseman 1950). The species' assignment to *Pratia* Gaudich. was occasioned by its baccate fruit; at that time *Pratia* was distinguished from *Lobelia* on the basis of producing berries instead of capsules.

The new species differed from most species of *Pratia* (and *Lobelia*) in producing a terminal bracteate raceme that was soon overtopped by an adjacent axillary shoot, causing the inflorescence to appear to have arisen in a lateral position. The only other herbaceous lobelioid to possess this unusual combination of baccate fruit and lateral inflorescence was the New Zealand endemic *P. physaloides* (A. Cunn.) Hemsl. These two species were also much larger plants than most other *Pratia* (a meter tall or more). Consequently, Hemsley (1886) placed the two species together as the sole members of *P. sect. Colensoa* (Hook. f.) Baill.

Wimmer (1943, 1953, 1968) expanded the circumscription of *Pratia* sect. *Colensoa* to include 11 additional species from southeastern Asia and the Neotropics. All were large baccate plants like the first two members, but bore solitary axillary flowers or terminal racemes instead of lateral racemes.

Moeliono (1960) transferred the Malesian species of *Pratia* (including *P. borneensis*) to *Lobelia*, arguing that fruit type was an inadequate basis upon which to distinguish genera among Campanulaceae. However, he did not concern himself with infrageneric classification and the precise relationships of the species within its new home were unstated. Murata (1995) resolved this uncertainty by transferring the sectional epithet from *Pratia* to *Lobelia*, creating *L. sect. Colensoa* (Hook. f.) J. Murata. He also expanded the circumscription of the section by adding a dozen species with capsular fruit from Brazil, tropical Africa, and tropical Asia to the baccate species included by Wimmer.

In the recent revision of *Lobelia* (Lammers 2010a), all of the species added to *L. sect. Colensoa* by Wimmer and Murata were removed and reassigned to *L. sect. Rhynchopetalum* (Fresen.) Benth., *L. sect. Speirema* (Hook. f.) Lammers, and *L. sect. Tylomium* (C. Presl) Benth. Furthermore, *L. borneensis* was judged to not be closely related to *L. physaloides* A. Cunn., and was likewise removed from *L. sect. Colensoa*; as it could not be accommodated in any other section (see below for details), it was segregated as monotypic *L. sect. Plagiobotrys*.

Although the type of *Lobelia borneensis* was collected in Sarawak, the majority of specimens come from farther east and north, in Sabah, particularly from the vicinity of Mt. Kinabalu. For many years, the species was considered endemic to Borneo. It was not until well into the Twentieth Century that plants identified as this species were discovered on the Indonesian islands of Sulawesi (Lam 1945), and Flores in the Lesser Sunda Islands (van Steenis 1967).

The only other name referable to *Lobelia* sect. *Plagiobotrys* is *Pratia borneensis* var. *grandiflora*. Kew botanist Otto Stapf based this on a specimen which George Darby Haviland collected on Mt. Kinabalu in March–April 1892 (Stapf 1894; van Steenis-Kruseman 1950; Beaman et al. 2001). Though recognized by Gibbs (1914), it was relegated to synonymy under the species by all subsequent authors (Wimmer 1953; Moeliono 1960; Beaman et al. 2001; Lammers 2007a).

MATERIALS AND METHODS

Morphological data were obtained from about 75 specimens in a dozen herbaria (see Acknowledgments) and analyzed via traditional taxonomic methodology (Leenhouts 1968; Qualls 1986; Vogel 1987; Maxted 1992; Watson 1997; Winston 1999). As I have done with other insular taxa (e.g., Lammers 2007c, 2009), I sought correlations between morphological variation and geographic distribution. Populations of *Lobelia borneensis* are known from just four discrete areas on three islands: (1) the Malaysian state of Sarawak on the island of Borneo at 425–1200 m, (2) the Malaysian state of Sabah on the same island at 975–3500 m; (3) the Indonesian island of Sulawesi at 900–1800 m, and (4) the Indonesian island of Flores in the Lesser Sunda Islands at 1600–1800 m. As in the prior studies, the initial hypothesis was that each area would harbor a single taxon unique to that locale, or at least to that island.

Therefore, when analyzing the data, I asked two questions. First, were all specimens from a given area relatively homogeneous, with most characters evincing a continuous pattern of variation? If so, the hypothesis would be supported; if instead, several characters consistently showed correlated gaps in their patterns of variation within an area, the hypothesis would be refuted. Second, were the plants with a given correlated suite of morphological features restricted to a single area or island? If so, the hypothesis would be supported; if not, the hypothesis would be refuted. Once taxa had been discerned in this fashion, they were compared to the nomenclatural type specimens to determine the correct name under the *International Code of Botanical Nomenclature* (McNeill et al. 2006). Decisions on rank for the taxa were made in light of the definitions of species and subspecies I have employed previously (e.g., Lammers 1991, 2005, 2007a).

RESULTS AND DISCUSSION

Relationships to other species.—As noted above, all previous authors have allied *Lobelia borneensis* to *L.*

physaloides, the type of *L.* sect. *Colensoa*. These are the only two species of *Lobelia* with lateral racemes, and they further share a moderately robust habit, large serrate petiolate leaves, corolla lobes several times longer than the tube, and baccate fruit. Nevertheless, I find it difficult to accept a close relationship between them.

The value of seed-coat structure in understanding relationships among Lobelioideae has been amply demonstrated (McVaugh 1936, 1940a, 1940b; Murata 1992, 1995; Buss et al. 2001; Lammers 2010). Variation in testal structure correlates well with variation patterns of other morphological features, as well as with phylogenies based on molecular data (Knox et al. 2006, 2008a, 2008b; Antonelli 2008; Givnish et al. 2009). It is largely testal structure that fails to support a close relationship between *Lobelia borneensis* and *L. physaloides*.

In *Lobelia physaloides*, the testa is striate, conforming to Murata Type D. This is by far the most common pattern in the genus, characterizing more than half its species. Its distribution in the more comprehensive molecular phylogenies (Knox et al. 2006; Antonelli 2008) supports Murata's (1992, 1995) hypothesis that it is the ancestral condition within the subfamily, from which each of the other types evolved independently. In contrast, the testa of *L. borneensis* is reticulate, conforming to Murata Type B. This pattern is far less common, occurring elsewhere only in the 43 species of amphi-Pacific *L.* sect. *Hypsela* (C. Presl) Lammers and in the sole species of *L.* sect. *Jasionopsis* Lammers, endemic to the West Cape region of South Africa. On this basis alone, one would hypothesize that *L. borneensis* and *L. physaloides* are not each other's closest relative.

In addition to seed-coat structure, the two species differ in other morphological features (Lammers 2010). In *Lobelia borneensis*, the stem is herbaceous to suffrutescent, scrambling or straggling, and up to 3 m long; that of *L. physaloides* is suffrutescent at base and fleshy above, erect to ascending, and no more than 1 m tall. Though both bear lateral racemes, those of *L. borneensis* are elongate, bearing as many as 35 flowers over the course of their development, while those of *L. physaloides* are subcorymbose, with rarely as many as 20 flowers. The pedicels in the former are bibracteolate below the middle, while those of the latter have several bracteoles along their length. The corolla of *L. borneensis* is 10–28 mm long with dorsal lobes only $\frac{2}{3}$ – $\frac{3}{4}$ as long as the ventral and laterally reflexed; that of *L. physaloides* is 30–45 mm long with the dorsal lobes equaling the ventral and erect. The tips of the anthers in *L. borneensis* are bearded with tufts of flattened hairs, while those of *L. physaloides* are nude or nearly so. Finally, the seeds of the former are cuboidal or quadrate and thus quite angular, while those of the latter are ovoid and terete. These numerous differences fail to support a close relationship between *L. borneensis* and *L. physaloides*, and support removal of the former from *L.* sect. *Colensoa*.

As noted above, some of the other baccate Asian species formerly assigned to *Pratia* sect. *Colensoa* have been removed to *Lobelia* sect. *Speirema* (Lammers 2010a, 2010b). These plants do resemble *L.* sect. *Plagiobotrys* in habit and in size and general structure of the flowers, and in an earlier draft of the revised classification, it was planned to assign *L. borneensis* there. However, these species differ in typically bearing solitary axillary flowers on ebracteolate pedicels, in having tufts of filiform hairs on the apex of the two ventral anthers, and in the striate-reticulate (Murata Type C) seed testa. In light of these differences, it seems best not to assign *L. borneensis* to *L.* sect. *Speirema*.

In light of their similarity in testal structure and fruit type, one might suggest that *L. borneensis* is referable to *L.* sect. *Hypsela*. These plants do resemble *L. borneensis* in their blue, purple, magenta, pink, or white corollas with the tube straight or nearly so and shorter than the lobes; many members have petiolate leaves, bibracteolate pedicels, and baccate fruit. However, these plants are far smaller, less than 0.4 m tall, often with stems prostrate or decumbent. Flowers are solitary in the axils of the upper leaves (rarely aggregated into a terminal raceme) and much smaller, with the corolla just 2–15 mm long. The corolla lobes are monomorphic or rarely somewhat dimorphic (vs. dimorphic) and the ventral anthers typically bear just a single long bristle each at apex. Though the seeds of both are reticulate, those in *L.* sect. *Hypsela* are ovoid to oblong and terete or rarely slightly compressed. For these reasons, *L. borneensis* was not assigned to *L.* sect. *Hypsela*, but instead segregated as a monotypic section.

Molecular data (Knox et al. 2006, 2008a; Antonelli 2008) indicate that *Lobelia physaloides* is derived from the endemic Australian taxon *L. sect. Holopogon* Benth.; like *L. sect. Hypsela*, this section consists of small often decumbent plants, rarely more than 0.4 m tall. One might hypothesize that in a parallel fashion, the larger *L. borneensis* evolved from smaller species referable to *L. sect. Hypsela*. Though *L. borneensis* has been sequenced (Givnish et al. 2009), it has yet to be included in the same cladistic analysis with *L. physaloides* or exemplars of *L. sect. Hypsela*. Doing so would test the hypothesis presented here.

Species and subspecies.—Careful analysis of the data supported the initial hypothesis: it is possible to determine consistently on the basis of morphology alone whether a specimen identified as *Lobelia borneensis* came from Sarawak, Sabah, Sulawesi, or Flores. Furthermore, in one of these areas (Sabah), two sets of populations can be distinguished on this basis, one occurring between 975–2900 m elevation, the other at 3000–3500 m. As a result of this finding, the originally monotypic *L. sect. Plagiobotrys* is here divided into five taxa: three allopatric on Sulawesi, Flores, and Sarawak, the other two parapatric in Sabah.

Most of the differences that serve to distinguish the five taxa involve floral characters, particularly the size, color, and posture of the corolla and staminal column. Such differences often are correlated with pollinator differences and thus may reflect mechanisms of reproductive isolation (Young 1982; Lammers & Freeman 1986; Lammers 1991, 2000, 2009; Thompson & Lammers 1997). As such, they are particularly useful in the taxonomy of the Lobelioideae.

The high-elevation plants on Sabah are the most distinctive of the five taxa, with flowers that are far more darkly pigmented and markedly larger: the ranges of values recorded for quantitative aspects of the hypanthium, corolla, and staminal column (see key below) show in almost all cases a definite gap between this taxon and the remainder. Such differences suggest to me that there is little or no gene flow between the two, despite their parapatry, i.e., they are reproductively isolated. As such, each merits specific rank. Although the four remaining taxa can be distinguished morphologically, the differences are less pronounced, with the ranges of quantitative floral features showing various degrees of overlap. This suggests to me that they are isolated primarily by geography and thus best treated as conspecific subspecies (cf. Lammers 1991, 2004, 2005, 2007c). As a result, *L. sect. Plagiobotrys* as recognized here comprises two species, one of which is divided into four allopatric subspecies.

As noted above, only two validly published names are referable to taxa in this section. The type of *Pratia borneensis* is a representative of the Sarawak taxon; as such, the more widespread species takes the name *Lobelia borneensis*, and its Sarawak subspecies is denoted by an autonym. The type of *P. borneensis* var. *grandiflora* represents the low-elevation Sabah taxon; the new combination *L. borneensis* subsp. *grandiflora* is here created for it. The species endemic to higher elevations in Sabah is here christened *L. origenes*, while appropriate names are likewise bestowed on the Sulawesi and Flores subspecies of *L. borneensis*.

TAXONOMY

Lobelia* sect. *Plagiobotrys Lammers, sect. nov. TYPE: *Lobelia borneensis* (Hemsl.) Moeliono.

Sectio a ceteris *Lobelieae* racemis elongatis pedunculatis lateralibus, trichomatibus applanatis insidens apicibus omnium quinque antherarum, fructibus baccatis, et seminibus cubiformibus vel quadratis cum testa reticulata (Typo B Muratae) distinguenda.

Plants perennial (hemicryptophytes or chamaephytes), 0.7–3 m tall, terrestrial. Stems herbaceous to suffrutescent, 2–5 mm diam., branched, straggling or scrambling, moderately leafy, glabrous or sparsely short-pubescent toward apex; latex acrid, viscous, white. Leaves alternate, simple, exstipulate, dorsiventral, pinnately veined (dillenid), petiolate; lamina broadly to narrowly elliptic, narrowly oblong, lanceolate, or ovate, chartaceous to subcoriaceous, glabrous adaxially, glabrous abaxially or short-pubescent on the veins; margin callose-serrate, callose-serrulate, or callose-denticulate, flat; apex acuminate to caudate; base cuneate, obtuse, or rounded; petiole much shorter than the blade. Flowers tetracyclic, perfect and proterandrous, zygomorphic, epigynous, pedicellate and resupinate, 5–35 in a terminal pedunculate bracteate raceme that appears lateral due to overtopping by a branch; axis elongate, short-pubescent; bracts linear, glabrous or short-pubescent; pedicels ascending, spreading, or deflexed, $\frac{2}{5}$ –3 times as long as its bract, bibracteolate

below middle, densely short-pubescent; bracteoles linear, inconspicuous. Calyx synsepalous, tube adnate to the ovary, forming an ellipsoid, broadly ellipsoid, campanulate, depressed ovate, or oblate hypanthium $\frac{1}{6}$ – $\frac{1}{3}$ as long as corolla, glabrous or short-pubescent, the base acute, obtuse, rounded, or truncate; lobes 5, valvate, tardily deciduous, linear-triangular or narrowly-triangular, equaling to 4 times as long as the hypanthium, spreading or erect, glabrous or sparsely short-pubescent, the margin entire, the apex acuminate. Corolla sympetalous, zygomorphic, bilabiate, cream-white suffused or marked with pink, blue, or purple, or red-purple or purple, short-pubescent inside and/or out; tube straight, cylindric, about as long as broad, dorsally cleft nearly to base; lobes 5, valvate, dimorphic; the two dorsal lobes oblong, narrowly oblong, or lanceolate, $1\frac{3}{4}$ – $7\frac{1}{2}$ times longer than the tube, reflexed laterally, the apex acute or acuminate; the three ventral lobes forming a trifold lip longer than the dorsal lobes and cleft for $\frac{1}{3}$ – $\frac{7}{8}$ its length, the segments narrowly oblong, narrowly elliptic, or lanceolate, acuminate at apex. Stamens 5, antisepalous, connate for most of their length; filament tube exerted at least slightly from dorsal slit of corolla, pubescent; dorsal anthers $\frac{1}{3}$ – $\frac{7}{8}$ as long as the filament tube and slightly longer than the ventral, overhanging the orifice of the tube and partly occluding it, all five bearded at apex with tufts of flattened white hairs 0.3–0.6 mm long, their surfaces glabrous or sparsely short-pubescent. Gynoecium syncarpous, bilocular; ovary inferior, adnate to the hypanthium for at least $\frac{2}{3}$ its length; placentae axile, large; ovules numerous, small, anatropous, unitegmic, tenuinucellate; style solitary, slender, terete, with a ring of stiff white hairs below the apex; stigma bilobed, the lobes appressed and non-receptive as the style grows through the anther tube, pushing out pollen, after which the stigmas spread and become receptive. Fruit a purple globose or oblate berry crowned by the calyx lobes; seeds tan, brown, or golden brown, cuboidal, broadly ellipsoid, broadly oblong, angular or slightly compressed, relatively small; testa reticulate (Murata Type B). Chromosome number unknown (Lammers 1993).

Etymology.—From the Greek *πλαγιος*, “placed sideways,” and *βοτρυς* “a bunch of grapes,” in allusion to the pedunculate lateral racemes of small purple berries.

KEY TO THE SPECIES AND SUBSPECIES

1. Hypanthium 6–7 mm long; corolla 25–29 mm long, red-purple, the dorsal lobes 15–20 mm long; filament tube 12–13 mm long; anther tube 1.8–2.2 mm diam, $\frac{1}{3}$ – $\frac{2}{5}$ as long as filament tube (Sabah) _____ **2. *L. origenes***
1. Hypanthium 2.5–5 mm long; corolla 10–22 mm long, white often tinged or marked with pink or purple, the dorsal lobes 6–15 mm long; filament tube 4–7 mm long; anther tube 1.2–1.8 mm diam, $\frac{3}{5}$ – $\frac{7}{8}$ as long as filament tube _____ **1. *L. borneensis***
2. Corolla 14–22 mm long, the dorsal lobes 7–15 mm, the ventral lip 12–21 mm long; filament tube 5–7 mm long; dorsal anthers 3.5–5 mm long (Sabah) _____ **1d. *L. borneensis* subsp. *grandiflora***
2. Corolla 10–17 mm long, the dorsal lobes 4–7 mm, the ventral lip 6–11 mm long; filament tube 4–5 mm long; dorsal anthers 2.5–3.5 mm long.
3. Hypanthium ellipsoid, 2–2.5 mm diam, the base obtuse; calyx lobes erect (Sarawak) _____ **1c. *L. borneensis* subsp. *borneensis***
3. Hypanthium oblate or depressed ovoid, 2.5–5 mm diam, the base truncate; calyx lobes spreading.
4. Abaxial veins of lamina densely pubescent; bracts 3–8 mm long, $\frac{1}{3}$ – $\frac{7}{8}$ as long as its pedicel; calyx lobes 2–4 times longer than hypanthium; corolla 10–13 mm long, the tube 1.8–3 mm diam, the dorsal lobes 1.7–2 mm wide, $2\frac{1}{4}$ – $3\frac{1}{2}$ times longer than tube (Sulawesi) _____ **1a. *L. borneensis* subsp. *celebensis***
4. Abaxial veins of lamina sparsely pubescent; bracts 8–23 mm long, equaling to $2\frac{1}{2}$ times longer than its pedicel; calyx lobes $1\frac{1}{2}$ – $2\frac{1}{3}$ times longer than hypanthium; corolla 12–17 mm long, the tube 3–3.5 mm diam, the dorsal lobes 1.3–1.5 mm wide, $1\frac{3}{4}$ –2 times longer than tube (Flores) _____ **1b. *L. borneensis* subsp. *insulae-florum***

1. *Lobelia borneensis* (Hemsl.) Moeliono in Steenis, Fl. Males. (ser. 1) 6:133. 1960. *Pratia borneensis* Hemsl.,

Hooker's Icon. Pl. 16: pl.1532. 1886. TYPE: MALAYSIA. SARAWAK: 1500 ft, Aug 1884, Hullet 256 (HOLOTYPE: K!).

Plants 0.7–3 m tall; stems glabrous or sparsely short-pubescent toward apex. Lamina broadly to narrowly elliptic, narrowly oblong, or ovate, 5 – 16.5×1.3 – 7 cm, chartaceous to subcoriaceous, glabrous adaxially, glabrous abaxially or short-pubescent on the veins; margin callose-serrate, callose-serrulate, or callose-den-

ticulate; apex acuminate to caudate; base cuneate or obtuse; petiole 7–25 mm long. Raceme 5–35-flowered; axis 2–24 cm long; bracts 3–23 × 0.3–1.1 mm, glabrous or short-pubescent; pedicels ascending, spreading, or deflexed, 5–15 mm long, $\frac{2}{5}$ as long to 3 times as long as its bract; bracteoles 0.5–2 mm long. Hypanthium ellipsoid, broadly ellipsoid, campanulate, depressed ovate, or oblate, 2–5 × 2–5 mm, $\frac{1}{6}$ – $\frac{1}{3}$ as long as corolla, glabrous or short-pubescent; base acute, obtuse, rounded, or truncate. Calyx lobes linear-triangular or narrowly-triangular, 4–12 × 0.5–1.8 mm, equaling to 4 times as long as the hypanthium, spreading or erect, glabrous or sparsely short-pubescent. Corolla cream-white suffused or marked with pink, blue, or purple, 10–22 mm long, short-pubescent inside and/or out; tube 2–4 × 1.5–3.5 mm; dorsal lobes oblong, narrowly oblong, or lanceolate, 4–15 × 1.3–3.5 mm, $1\frac{3}{4}$ – $7\frac{1}{2}$ times longer than the tube, the apex acute or acuminate; ventral lip 6–21 mm long, cleft for $\frac{1}{3}$ – $\frac{7}{8}$ its length, the segments narrowly oblong or lanceolate, 1.5–4 mm wide. Filament tube 4–7 mm long; anther tube 1.2–1.8 mm diam., its surface sparsely short-pubescent toward apex dorsally; dorsal anthers 2.5–5 mm long, $\frac{1}{2}$ – $\frac{7}{8}$ as long as the filament tube; ventral anthers 2–4 mm long. Berry globose or oblate, 4–13 × 6–14 mm; seeds brown or golden brown, cuboidal or broadly oblong, angular or slightly compressed, 0.7–0.9 × 0.5–0.8 mm (Murata Type B).

Distribution.—Represented by four allopatric subspecies, on Flores, Sulawesi, and Borneo.

1a. *Lobelia borneensis* subsp. *celebensis* Lammers, subsp. nov. (**Fig. 1A**). TYPE: INDONESIA. SULAWESI: Todjambö-gebüsch im Regenwald, 900 m, 28 Jun 1929, Dr. G. Kjellberg 1818 (HOLOTYPE: S!).

Plantae Celebis a plantis Lobeliae borneensis insularum ceterarum nervis abaxialibus foliarum dense pubescentibus, bracteis floralibus 3–8(–12) mm longis cum pedicellis ascendentibus, hypanthio oblata basi truncato cum calycis lobis patentibus, et corollae lobis 2.2–3.5 plo corollae tubo longioribus distinguenda.

Plants 2–3 m tall, glabrous or sparsely short-pubescent toward apex. Lamina elliptic or narrowly oblong, 7–15 × 2.3–5.2 cm, densely short-pubescent on abaxial veins; margin callose-serrulate; apex acuminate, base cuneate or obtuse; petiole 10–22 mm long. Raceme 10–28-flowered; axis 5–24 cm long, moderately to densely short-pubescent; bracts 3–8 × 0.5 mm, sparsely short-pubescent; pedicels ascending, 6–12 mm long, equaling to $2\frac{1}{2}$ times as long as its bract. Hypanthium oblate, 2–2.5 × 2–4 mm, $\frac{1}{5}$ – $\frac{1}{4}$ as long as corolla, sparsely short-pubescent; base truncate. Calyx lobes linear-triangular or narrowly triangular, 4–12 × 0.5–1.7 mm, 2–4 times as long as the hypanthium, spreading, glabrous. Corolla cream-white suffused with blue or purple, 10–13 mm long, sparsely to densely short-pubescent externally; dorsal lobes oblong, 4–7 × 1.8–2 mm, $2\frac{1}{4}$ – $3\frac{1}{2}$ times longer than the tube; ventral lip 6–11 mm long, cleft for $\frac{1}{2}$ – $\frac{4}{5}$ its length, the segments lanceolate, 1.5–2 mm wide. Filament tube 4–5 mm long; anther tube 1.5–1.6 mm diam.; dorsal anthers 2.5–3.5 mm long, $\frac{1}{2}$ – $\frac{7}{8}$ as long as the filament tube; ventral anthers 2–2.5 mm long. Seeds cuboidal, angular, 0.7–0.8 × 0.5–0.6 mm.

Distribution, habitat, and phenology.—Endemic to the island of Sulawesi in Indonesia. Wet montane forests, 900–1800 m. Flowering and fruiting January through August.

Etymology.—From *Celebes*, the name bestowed on the island by Portugese navigators, and the Latin geographical suffix *-ensis*.

Discussion.—This subspecies is distinctive by virtue of the dense pubescence on the abaxial leaf veins; in the other subspecies, the pubescence is much sparser or even absent and the hairs sometimes far smaller. Its oblate truncate hypanthium and spreading calyx lobes are shared with the next subspecies, and distinguish the extra-Bornean taxa collectively.

Representative specimens: **INDONESIA. SULAWESI**: Masamba, Limboeng-Maboesa, Eyma 1165 (K, L); Masamba, between Tetahi and Toeke-aho-pass, Eyma 1552 (L); Poso, Maraowa, N side, Eyma 1552bis (L); onder afd. Makale, Rantepao, Toradjalanden, C. Monod de Froideville 192 (L); G. Batoe, Rachmat 435 (L); G. Katonghoan, Rachmat 1007 (L).

1b. *Lobelia borneensis* subsp. *insulae-florum* Lammers, subsp. nov. (**Fig. 1B**). TYPE: INDONESIA. LESSER SUNDRA ISLANDS: Flores, Ruteng, Lusang Pass, steep rocky slopes, hanging from steep cliff, 1600 m, 16 Jun 1975, J.F. Veldkamp 7007 (HOLOTYPE: [on two sheets]: L! ISOTYPE: MO!).

Plantae Insulae Florum a plantis Lobeliae borneensis insularum ceterarum nervis abaxialibus foliarum sparse pubescentibus, bracteis flo-

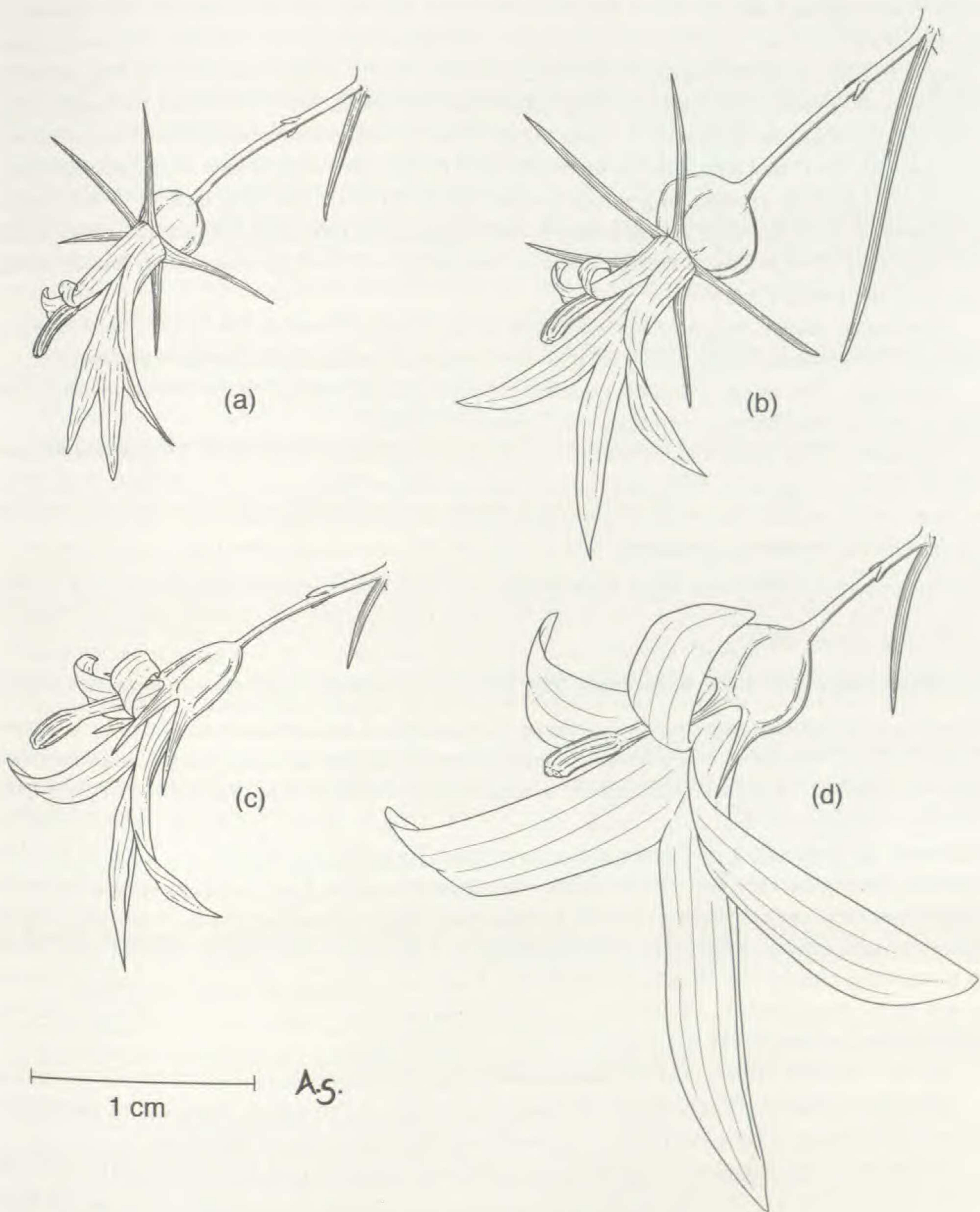


FIG. 1. Flowers of the subspecies of *Lobelia borneensis* (based on the respective holotypes). A. *Lobelia borneensis* subsp. *celebensis*. B. *Lobelia borneensis* subsp. *insulae-florum*. C. *Lobelia borneensis* subsp. *borneensis*. D. *Lobelia borneensis* subsp. *grandiflora*.

calicibus 8–23 mm longis cum pedicellis ascendentibus, hypanthio oblata vel depresso-ovata basi truncato cum calycis lobis patentibus, et corollae lobis sesqui- vel duplo corollae tubo longioribus distinguenda.

Plants 1–3 m tall; stems glabrous. Lamina elliptic, 6–16 × 1.9–5.6 cm, sparsely short-pubescent on abaxial veins; margin callose-serrate, callose-serrulate, or callose-denticulate; apex acuminate; base cuneate or obtuse;

petiole 17–25 mm long. Raceme 28–35-flowered; axis 12–15 cm long, sparsely to densely short-pubescent; bracts 8–23 × 0.6–1.1 mm, sparsely short-pubescent; pedicels ascending, 7–13 mm long, $\frac{2}{5}$ as long to about as long as its bract. Hypanthium depressed ovate or oblate, 2.5–4.5 × 2.5–5 mm, $\frac{2}{5}$ – $\frac{1}{3}$ as long as corolla, short-pubescent in lines; base truncate. Calyx lobes linear-triangular, 5–9 × 1–1.2 mm, half again as long to $2\frac{1}{2}$ times as long as the hypanthium, spreading, glabrous. Corolla cream-white suffused or marked with blue or purple, 12–17 mm long, sparsely short-pubescent in lines externally; dorsal lobes narrowly oblong, 6–7 × 1.3–1.5 mm, $1\frac{1}{2}$ –2 times longer than the tube; ventral lip 10–11 mm long, cleft for $\frac{1}{3}$ – $\frac{7}{8}$ its length, the segments 1.5–2.5 mm wide. Filament tube 4–5 mm long; anther tube 1.4–1.5 mm diam.; dorsal anthers 3–3.5 mm long, $\frac{2}{3}$ – $\frac{3}{4}$ as long as the filament tube; ventral anthers 2.5–3 mm long. Seeds broadly oblong, slightly compressed, 0.8 × 0.6 mm.

Distribution, habitat, and phenology.—Endemic to the island of Flores in the Lesser Sunda Islands of Indonesia. Wet montane forests, 1600–1800 m. Flowering and fruiting April through September.

Etymology.—The subspecific epithet is a Latin genitive phrase translating the Portuguese name of the island to which the subspecies is endemic, i.e., “island of flowers.”

Discussion.—This subspecies is distinctive in the great length of its bracts (up to 23 mm long and more than $2\frac{1}{2}$ times as long as the subtended pedicel) and the relative brevity of its dorsal corolla lobes (twice the length of the corolla tube or less). It resembles *Lobelia borneensis* subsp. *celebensis* in its oblate truncate hypanthium and spreading calyx lobes.

Representative specimens: **INDONESIA. Lesser Sunda Islands:** Flores, Manau near Ruteng, *Kostermans & Wirawan* 651 (K, L); Flores, Ruteng, Kl. Soenda, *Father E. Schmutz* 482 (L); Flores, Ruteng, Mt. Kasteno, *Father E. Schmutz* 3227 (L); Flores, *Father J.A.J. Verheijen* 2175 (L), *Father J.A.J. Verheijen* 2857 (L).

1c. *Lobelia borneensis* subsp. *borneensis*. (Fig. 1C). Autonym created here by publication of the other three subspecies.

Plants 0.9–1.2 m tall; stems sparsely short pubescent toward apex. Lamina broadly elliptic, elliptic, or ovate, 7.5–16.5 × 3.2–7 cm, glabrous or minutely sparsely pubescent on abaxial veins; margin callose-serrulate; apex short-caudate or acuminate; base cuneate or obtuse; petiole 9–18 mm long. Raceme 7–23-flowered; axis 7.5–19 cm long, densely short-pubescent; bracts 3–7 × 0.3–0.5 mm, sparsely pubescent; pedicels spreading to deflexed, 5–15 mm long, $\frac{7}{8}$ –3 times as long as its bract. Hypanthium ellipsoid, 3 × 2.3 mm, $\frac{1}{4}$ as long as corolla, short-pubescent; base obtuse. Calyx lobes linear-triangular, 4 × 0.5 mm, $\frac{1}{3}$ again as long as the hypanthium, erect, sparsely short-pubescent. Corolla cream-white suffused with blue, 12 mm long, sparsely short-pubescent within; dorsal lobes narrowly oblong, 6 × 1.5 mm, 3 times longer than the tube; ventral lip 10 mm long, cleft for $\frac{3}{5}$ its length, the segments 1.5 mm wide. Filament tube 4–5 mm long; anther tube 1.2 mm diam.; dorsal anthers 2.5 mm long, $\frac{3}{5}$ – $\frac{2}{3}$ as long as the filament tube; ventral anthers 2.2 mm long. Seeds cuboidal or broadly oblong, angular, 0.7–0.9 × 0.6–0.7 mm.

Icones.—Hemsley (1886), pl. 1532; Murata (1995), figs. 30–31 [seed].

Distribution, habitat, and phenology.—Endemic to the state of Sarawak in Malaysia, on the island of Borneo. Wet montane forests and riverine forests, 425–1200 m. Flowering in September.

Discussion.—This subspecies is distinctive in its deflexed or spreading pedicels; those of the other three subspecies are ascending. Its ellipsoid hypanthium obtuse at base and the erect calyx lobes are also found in the other Borneo taxon, *Lobelia borneensis* subsp. *grandiflora*. However, it resembles *L. borneensis* subsp. *celebensis* and *L. borneensis* subsp. *insulae-florum* in having flowers much smaller than in that subspecies.

Representative specimens: **MALAYSIA. SARAWAK:** Kuching District, Mount Penrissen, N side, *J.H. Beaman et al.* 11888 (K); Matang, *Dr. G.D. Haviland* 577 (K); Bkt. Kumbong, Btg. Balui, Kapit, *Runi et al.* 62049 (MO).

1d. *Lobelia borneensis* subsp. *grandiflora* (Stapf) Lammers, comb. et stat. nov. (Fig. 1D). *Pratia borneensis* var. *grandiflora* Stapf, Trans. Linn. Soc. London, Bot. 4: 188 (1894). TYPE: MALAYSIA. SABAH: Dahombang, seldom flooded part of bed, 3000 ft, *Dr. G.D. Haviland* 1309 (HOLOTYPE: K! ISOTYPE: K!).

Plants 0.7–2 m tall; stems glabrous or sometimes sparsely short pubescent toward apex. Lamina broadly to narrowly elliptic, 5–15 × 1.3–5.2 cm, minutely sparsely pubescent on abaxial veins; margin callose-serrulate

to callose-serrate; apex caudate or acuminate; base cuneate; petiole 7–20 mm long. Raceme 5–22-flowered; axis 2–15 cm long; bracts 6–11 × 0.5–1 mm, glabrous or sparsely short-pubescent; pedicels ascending, 5–10 mm long, $\frac{2}{3}$ as long to a little longer than its bract. Hypanthium broadly ellipsoid or campanulate, 3–5 × 2.5–4 mm, $\frac{1}{6}$ – $\frac{1}{4}$ as long as corolla, glabrous or sparsely short-pubescent; base acute, obtuse, or rounded. Calyx lobes linear-triangular to narrowly-triangular, 4–8 × 0.7–1.8 mm, equaling to $2\frac{1}{4}$ times as long as the hypanthium, erect, glabrous. Corolla cream-white suffused or marked with pink or purple, 14–22 mm long, pubescent within; dorsal lobes oblong or lanceolate, 7–15 × 1.5–3.5 mm, 3–7½ times longer than the tube; ventral lip 12–21 mm long, cleft for $\frac{1}{2}$ – $\frac{3}{4}$ its length, the segments 1.5–4 mm wide. Filament tube 5–7 mm long; anther tube 1.2–1.8 mm diam.; dorsal anthers 3.5–5 mm long, $\frac{3}{5}$ – $\frac{4}{5}$ as long as the filament tube; ventral anthers 2.5–4 mm long. Seeds broadly ellipsoid, slightly compressed, 0.8–0.9 × 0.7–0.8 mm.

Icones.—Wimmer (1943), fig. 30b; Beaman et al. (2001), pl. 12D.

Distribution, habitat and phenology.—Endemic to the state of Sabah in Malaysia. Wet montane forests, 975–2900 m. Apparently flowering and fruiting year-round.

Vernacular names.—Dusun: akar maga pawang.

Discussion.—The flowers of this subspecies are by far the largest in *Lobelia borneensis*, approaching in size those of its sister-species, *L. origenes*. Of the other subspecies, it is most similar to *L. borneensis* subsp. *borneensis* by virtue of its ellipsoid hypanthium obtuse at base and its erect calyx lobes.

Representative specimens: **MALAYSIA. SABAH**: S slope of Mt. Kinabalu, ca 5 mi NW of Kundasan, L. B. Abbe et al. 9982 (NY); Mt. Kinabalu National Park, Liwagu River drainage, E. F. Anderson 4318 (MO); Tambunan, Crocker Range, Km 55.4 on Kota Kinabalu – Tambunan Road, J.H. Beaman et al. 7298 (K, L, MO, MSC, NY); Ranau, Pinosuk Plateau, East Mesilau River, J.H. Beaman et al. 8548 (CAS, L, MO, MSC, NY); Tambunan, Crocker Range, Km 58.2 on Kota Kinabalu – Tambunan Road, J.H. Beaman et al. 8898 (L, MSC); Kundasan, vicinity of Forest Rest House, A. L. Bogle et al. 356 (NY); Mt. Kinabalu, vicinity of Kambaranga, A. L. Bogle et al. 396 (NY); S slope Mt. Kinabalu, trail from Mesilau Cave to Janet's Halt, S. Collette 21639 (K, L); Mt. Kinabalu National Park, road to summit, T. B. Croat 53125 (MO); Mt. Kinabalu, Tenompok, J. Clemens & M. S. Clemens 27474 (B, F, L, M, NY); Mt. Kinabalu, Colombon River, J. Clemens & M. S. Clemens 35055 (L, NY); Upper Kinabalu, Gurulau spur, J. Clemens & M. S. Clemens 50943 (NY); Mt. Kinabalu, below Kamburango, F. R. Fosberg 44126 (OSH); Ranau, Tenompok, M. Kadir A1665 (K, L); Ranau, Kinabalu Nat. Park behind Hqrs., A. Kanis 50114 (K); Penampang, road from Agr. Exp. Station to south of G. Alab, S. Kokawa & M. Hotta 1829 (L); Kinabalu National Park, road between HQ and Tenompok, S. Kokawa & M. Hotta 3041 (L); Ranau, Tenompok, W. Meijer 20309 (L); G. Alab, 22 Feb 1969, H. P. Nooteboom 986 (B, L); Kinabalu, power station, W. R. Price 153 (K); Mt. Kinabalu, Lumu-lumu, J. Sinclair et al. 9218 (L, M); Mt. Kinabalu, near radio station, J. B. Smith 565 (L); Ranau, Kinabalu National Park, Silam-Silam trail, P. F. Stevens et al. 679 (L); route up to G. Alap, Tambunan, J. B. Sugau 67 (HAST); Ranau, Mesilau, M. Ubaldus 131286 (K); Tenompok, Anin et al. 123409 (K).

2. *Lobelia origenes* Lammers, sp. nov. (Fig. 2). TYPE: MALAYSIA. SABAH ["North Borneo"]: Mt. Kinabalu, eastern shoulder, from head of valley at entrance to Shangri-La valley, very damp and shady, forming dense low thicket, above Camp V, ca 11,500 ft, 5 Aug 1961, Mrs. Collette 791 (HOLOTYPE: K!).

Plantae ob racemos laterales nunantes et baccas atrovioleas *Lobeliae borneensi* valde simulantes sed montes superiores incolentes; floribus grandioribus cum hypanthio 6–7 mm longo, corolla atrovinosa 25–29 mm longa, corollae lobis dorsalibus 12–13 mm longis, et antherarum tubo 1.8–2.2 mm diametro longitudine $\frac{1}{3}$ – $\frac{2}{5}$ filamentorum tubi aequanti distinguenda.

Plants 1–1.5 m tall; stems glabrous. Lamina ovate, lanceolate, or elliptic, 7–12 × 2.3–4.4 cm, subcoriaceous, glabrous or minutely sparsely pubescent on veins abaxially; margin minutely callose-denticulate; apex acuminate; base rounded, obtuse, or cuneate; petiole 5–17 mm long. Raceme 6–11-flowered; axis 7–11 cm long; bracts 10–18 mm × 0.5–1.4 mm, glabrous, the margin entire; pedicels ascending, 9–14 mm long, equaling to a bit shorter than the subtended bract; bracteoles 1.5–2 mm long. Hypanthium ellipsoid, 6–7 × 4.5–5.5 mm, $\frac{1}{4}$ as long as corolla, sparsely short-pubescent; base acute or obtuse. Calyx lobes narrowly triangular, 7–10 × 1.3–1.8 mm, equaling to half again as long as the hypanthium, erect, glabrous. Corolla red-purple or purple, 25–28 mm long, sparsely short-pubescent inside and out; tube 3.5–4.5 × 3.5–4 mm; dorsal lobes narrowly oblong, 15–20 × 2–2.5 mm, $3\frac{1}{2}$ –5 times longer than the tube, apex acute; ventral lip 21–23 mm long, cleft for $\frac{3}{4}$ – $\frac{7}{8}$ its length, the segments narrowly elliptic, 3–3.3 mm long. Filament tube 12–13 mm long; anther tube, 1.8–2.2 mm diam., its surface glabrous or sparsely short-pubescent at base; dorsal anthers 5–5.5 mm long, $\frac{1}{3}$ – $\frac{2}{5}$ as long as the filament tube; ventral anthers 4–4.5 mm long. Berry globose, 15–16 × 15–16 mm; seeds tan, oblong or broadly ellipsoid, angular or slightly compressed, 1–1.2 × 0.7–0.8 mm.



FIG. 2. *Lobelia origenes*. A. Berry (based on Chew et al. 880 (K). B. Flowering branch (based on the holotype).

Distribution, habitat, and phenology.—Endemic to the eastern shoulder of Mt. Kinabalu on northern Borneo, in the Malaysian state of Sabah. Evergreen broadleaf forest, 3000–3500 m; flowering and fruiting July–August.

Etymology.—From the Greek ὄρειγενής, “mountain-born,” in reference to its hypothesized origin as a high-elevation derivative of *L. borneensis*.

Discussion.—These specimens were originally identified as *Lobelia borneensis*, and the type was cited under that name by Beaman et al. (2001). That species also occurs on Kinabalu, but only at elevations of 975–2900 m; it would seem to be the progenitor of *L. origenes*. The pronounced gap in corolla size and color and in filament column length, in addition to the elevational separation, suggest that the two are reproductively isolated by pollinator differences.

Representative specimens: **MALAYSIA. SABAH:** Mt. Kinabalu, eastern shoulder, Chew et al. 880 (K, L).

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